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The spatial association of blue whales (*Balaenoptera musculus*) with krill patches (*Thysanoessa* spp. and *Meganyctiphanes norvegica*) in the estuary and northwestern Gulf of St. Lawrence

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The St. Lawrence Estuary is known as a summer foraging area for several species of marine mammals, including several species of rorquals. Among these is the blue whale, which feeds almost exclusively on euphausiids. Therefore, the abundance, distribution and local density of krill should logically be a strong explanatory variable for the distribution of blue whales. However little is known about the spatial association of blue whales with the aggregation dynamics of krill in eastern Canada. Six years of acoustic surveys of which four were combined with marine mammal observations were undertaken to study the medium- and small-scale distribution of blue whales and krill within the northwestern Gulf of St. Lawrence and estuary. We show that there are several areas of krill aggregation throughout the study area that are frequented by blue whales in summer on a recurring and, at times, intensive basis, i.e. by several whales at the same time. Krill aggregations in these areas vary inter-annually in biomass and species composition. In addition, we show that the distribution of blue whales is more strongly associated with the density distribution of *Thysanoessa* spp. (predominantly *T. raschii*) than *Meganyctiphanes norvegica*. Densities of blue whales were greatest in slope areas where *T. raschii* preferentially aggregate. *T. raschii* forms denser aggregations and is distributed higher in the water column than *M. norvegica*, resulting in more biomass available to air-breathing predators at lesser energetic cost. In particular, we show that blue whales are specifically associated with shallow water krill swarms (0-80 m) more than all other krill configurations during daytime. This suggests that blue whales are not necessarily attracted to areas of high total biomass or the highest integrated density of krill aggregations, but rather to areas of more accessible krill biomass of which shallow-water, daytime swarms are disproportionately selected.

Association spatiale des baleines bleues (*Balaenoptera musculus*) avec des taches de krill (*Thysanoessa* spp. et *Meganyctiphanes norvegica*) dans l'estuaire et le nord-ouest du golfe du Saint-Laurent

RÉSUMÉ

L'estuaire du Saint-Laurent est reconnu comme une zone d'alimentation estivale pour plusieurs espèces de mammifères marins, y compris plusieurs espèces de rorquals. Parmi ceux-ci, on compte le rorqual bleu, qui se nourrit presque exclusivement d'euphausiacés. Par conséquent, l'abondance, la répartition et la densité locale du krill devraient logiquement être une variable explicative dominante pour la répartition des rorquals bleus. Cependant, on en connaît peu sur l'association spatiale des rorquals bleus par rapport à la dynamique d'agrégation du krill dans l'est du Canada. Six années de relevés acoustiques, dont quatre étaient combinées avec l'observation de mammifères marins, ont été entreprises pour étudier la répartition du rorqual bleu à petite et moyenne échelle dans l'estuaire et le nord-ouest du golfe du Saint-Laurent. L'étude révèle que plusieurs des zones d'agrégation du krill observées sont fréquentées par des rorquals bleus durant l'été, de façon récurrente et parfois intense, c'est-à-dire par plusieurs baleines en même temps. La biomasse et le type d'espèces des agrégations de krill dans ces zones varient d'une année à l'autre. L'étude démontre également que la répartition des rorquals bleus est plus fortement associée à la répartition de la densité du *Thysanoessa* spp. (principalement *T. raschii*) que de *Meganyctiphanes norvegica*. Les densités des rorquals bleus étaient plus grandes dans les eaux du talus où *T. raschii* se concentre préférentiellement. *T. raschii* forme des agrégations plus denses et se retrouve plus haut dans la colonne d'eau que *M. norvegica*, ce qui signifie que les prédateurs à respiration aérienne ont accès à une plus grande biomasse en dépensant moins d'énergie. L'étude révèle en particulier que, durant le jour, la répartition des rorquals bleus est plus souvent associée aux essaims de krill en eaux peu profondes (entre 0 et 80 m) qu'à toutes autres configurations de krill. On peut donc en déduire que les rorquals bleus ne sont pas nécessairement attirés par les zones à forte biomasse totale ou par les endroits où la densité intégrée des agrégations de krill est la plus élevée, mais plutôt aux zones où la biomasse du krill est plus facilement accessible, des zones parmi lesquelles les essaims de krill diurnes en eaux peu profondes sont disproportionnellement sélectionnés.

INTRODUCTION

The Canadian Species at Risk Act (SARA) requires the definition of critical habitat for species listed as 'endangered', including the western North Atlantic (WNA) blue whale (*Balaenoptera musculus*). The challenge is to determine what fraction of the vast territory occupied by the WNA blue whale and other large rorquals is critical to them. The recovery strategy for WNA blue whales (Beauchamp et al. 2009) has identified research topics for which new information is required to improve our limited knowledge of important areas related to reproduction, migration and feeding. The goal of the present study is to identify the characteristics that define important feeding habitat.

Many rorquals come specifically and repeatedly to the estuary and Gulf of St. Lawrence (GSL) in the ice-free months (Comtois et al. 2010, Lesage et al. 2007) to feed on pelagic species of fish as well as meso- and macrozooplankton, especially krill. This latter prey group, particularly sought by blue whales, is comprised of four species in the WNA, although in the GSL its biomass is dominated by northern krill (*Meganyctiphanes norvegica*) and the smaller but more gregarious Arctic krill (*Thysanoessa* spp.) (Berkes 1976). Assuming that the blue whales that enter the GSL are foraging for the best krill aggregations within its territory, the abundance, distribution and local density of northern and Arctic krill should logically be one of the main factors determining the distribution of foraging blue whales, as well as other baleen whales for which krill is also a major prey. Therefore, defining important feeding habitat for the largest of marine predators should be a fairly simple matter of describing the characteristic that most directly defines their feeding habitat – krill distribution and abundance. However the distribution of krill abundance has been difficult to measure and quantify in the past due to net avoidance issues (Brierley et al. 2003, Brinton 1967, Hovekamp 1989, Ianson et al. 2004, Wiebe et al. 1982) and krill patches are not typically spatially and temporally stable. However, recent methodological advances such as the use of stroboscopes (Sameoto et al. 1993, Wiebe et al. 2013) and acoustic multifrequency classification (Lawson et al. 2008, McQuinn et al. 2013a) have allowed for the efficient quantification of krill biomass from very local to basin scales.

Most of our information concerning the distribution and movements of blue whales comes from the northwestern GSL and particularly the St. Lawrence estuary (SLE) (Ramp and Sears 2012). Within this region, blue whales have historically been abundant (e.g. Kingsley and Reeves 1998, Lawson and Gosselin 2009, Lesage et al. 2007, Sears and Williamson 1982) as well as accessible for both the whale-watching industry and marine-mammal scientists compared to the eastern GSL. Areas where blue whales are known to frequent are the Quebec north shore, centered on the Mingan Archipelago, the head of the Laurentian Channel (HLC) in the SLE, and the tip of the Gaspé Peninsula (Fig 1). The annual migration patterns of blue whales into the GSL are known in a general sense. Evidence suggests that they enter the GSL via Cabot Strait and are seen first off Gaspé in the spring and early summer. Few blue whales are seen in the SLE before mid-July and their visitations tend to peak in August and September, although there is little sighting effort past this period. However, interannual variability in the abundance of blue whales within these areas is very high and unpredictable (Comtois et al. 2010).

Further, little was known until recently about the distribution and aggregation dynamics of krill within the GSL. McQuinn et al. (2015) and Maps et al. (2015) have shown that the estuary is only one of many choices of foraging habitat for blue and other baleen whales in the GSL. There are areas of significant krill biomass throughout the GSL that until recently were virtually unsurveyed, where WNA blue whales can potentially forage without detection.

Many studies have shown the general association between marine mammals and their prey (e.g. Baumgartner et al. 2003, Macaulay et al. 1995, Murison and Gaskin 1989, Santora et al.

2010). Most of these studies have examined the overlap of average prey fields with the distribution of various marine mammals and have concluded that there were strong associations between them on a broad scale. However, very few studies have investigated the association between rorquals and their prey fields simultaneously (but see Croll et al. 2005). Some studies lacked the spatial resolution of the prey; others lacked the synchronicity of data collection of predator and prey. However, prey fields may change quickly, in the order of hours or days, which may explain the documented ephemeral appearance and disappearance of rorquals in particular sectors. Therefore, there is a need to understand the specific nature of the association between these large baleen whales and the krill that defines their habitat on finer spatial and temporal scales.

We combined six years of acoustic mapping of krill by species and four years of simultaneous marine-mammal observation data (MMO) from regional-scale surveys within the GSL, to study the medium- and fine-scale associations between large rorquals and their prey, with special focus on blue whales. Our objectives were to determine the strength of the association between the distribution of these cetacean species and krill aggregation characteristics to identify the factors involved in determining prey choice, to be used to better define habitats that are important, and potentially critical, to blue whales.

MATERIAL AND METHODS

REGIONAL-SCALE SURVEYS

Six annual, regional-scale acoustic surveys were conducted in August from 2009 to 2014 with concurrent MMO data collection in all but two years (2010 and 2014) with the objective of describing the medium- to fine-scale species-specific, spatial abundance and distribution of both cetaceans and the forage species comprising their prey. We defined a study area that would include an ecologically significant fraction of the krill population without over-extending our spatial coverage and reducing resolution beyond the scale of krill patches. The slope area along the shelf breaks on either side of the Laurentian Channel was considered high potential habitat for krill (Sameoto 1975, 1976, Simard et al. 1986). Further, McQuinn et al. (2015) determined that significant krill patches aggregated northeast of Anticosti Island, in the Anticosti Gyre to the west, in the Pentecôte area at the mouth of the estuary, along the north and south shores of the SLE, in the Gaspé Current and off Gaspé. It was therefore decided that the surveys would cover the lower SLE east to the northwestern GSL (Fig 1) from Anticosti Island to Gaspé (>18000 km^2), concentrating along the slope where most krill aggregation had been found previously (McQuinn et al. 2015).

SURVEY DESIGN

The survey design is described in McQuinn et al. (2015). Basically the surveys were stratified-random transect surveys (Jolly and Hampton 1990) with one exception; the parallel transects were chosen systematically, i.e. equidistant from a random starting point for each stratum. These surveys had a fine spatial resolution, with transects spaced 10 - 20 km apart depending on stratum priority, generally oriented perpendicularly to the coast to cross the krill density gradient. With this resolution, we were able to define aggregation dimensions and extent with reasonable detail.

Survey lines were run in daylight hours only when krill is expected to be at their daytime depth, i.e. > 100 m and below the photic zone (Plourde et al. 2013), and to be well within the range of the acoustic beam (4.5 > range < 220 m), i.e. not in the upper-surface layer above the transducers. It is recognized however, that krill can form swarms in the upper water column (<

100 m) during the day that can, on occasion, be very close to the surface and therefore at least partially above the transducers. Finally, the two dominant krill species have shown little vertical overlap during daytime (McQuinn et al. 2013a), thereby minimizing mixed krill scattering layers.

ACOUSTIC DATA COLLECTION

Multifrequency acoustic S_v data was recorded during the entire time of each survey from a Simrad® EK60 multifrequency echosounder (38, 70, 120, 200 and 333 kHz) installed aboard a SWATH (SwathOceans®) research vessel, the *FG Creed*. This system was calibrated *in situ* in all years at the beginning of each survey season[1] using a 38.1 mm tungsten-carbide (6% cobalt binder) standard sphere for the 4 lower frequencies, and a 22.0 mm tungsten-carbide sphere for the 333 kHz transceiver. Calibration results were similar in all years.

PREY CLASSIFICATION

Macrozooplankton prey were classified acoustically into krill species, *Meganyctiphanes norvegica* and *Thysanoessa* spp. (of which *T. raschii* was dominant), as described by McQuinn et al. (2013a). These authors showed that the two principle krill species had distinctive frequency responses at 38, 120 and 200 kHz, due in large part to their non-overlapping length distribution as adults, which allowed for effective discrimination of krill scattering layers. The classification technique uses the difference in pairs of S_v binned values from 38, 120 and 200 kHz data:

$$\Delta S_{v,x-y} = S_{v,x} - S_{v,y}$$

where x is the upper frequency and y is the lower, to describe empirically the acoustic frequency response of a species or species group (McQuinn et al. 2013a). For *M. norvegica* and *T. raschii*, the classifications were validated with independent net sampling and physical modelling.

MARINE MAMMAL OBSERVATIONS

During the four surveys included in our analyses, observers collected whale sighting data during daylight hours at an approximate vessel speed of 12 kt. One or two marine mammal observers were set up outside on the highest bridge possible enabling an unobstructed view of at least 180° in front of the vessel, or from the wheelhouse when weather conditions prevented safe observation conditions from outside stations. Vessel position was recorded every second to ten seconds using a portable GPS (Garmin, GPSMAP76 or GPSMAP78s). Observers scanned the water surface with naked eyes and were instructed to collect distance sampling data (Buckland et al. 2015). Once a group of marine mammals was detected, 7x50 binoculars (Bushnell, Marine) could be used to help with the identification of species and the estimation of the number of individuals in the group. Radial distance of the sighting from the vessel was measured using the same 7x50 binoculars equipped with reticles, or using an inclinometer if the sighting was too close to allow simultaneous observation of both the sighting and the horizon in the binocular's field of view. As a third option, the distance was estimated visually when animals were close to the vessel and passing too quickly to allow the use of measuring instruments. The radial distance was estimated using the equation from Lerczack and Hobbs (1998). The horizontal angle relative to the vessel bearing was also measured using a simple protractor fixed to the vessel. All of the information was recorded by each observer on digital voice recorders or in field books. All observations were recorded with the time synchronized to the GPS allowing the estimation of the exact position of each marine mammal sighting relative to the position of the

[1]The exception was 2011, in which a post-calibration was conducted in mid-season

vessel using the relative angle from the vessel bearing and the radial distance. All sightings were crosschecked between observers to prevent the recording of duplicate sightings.

Sighted marine mammals were identified to the most precise taxonomic group possible, usually to species. If identification to species was ambiguous, the individuals were classified to the nearest group that information would allow, e.g. large rorqual.

AREAL EXTENT OF KRILL PATCHES

For this study, we assumed that the primary feature of interest to a foraging blue whale was the krill 'patch'. Here a patch is defined as an accumulation of prey organisms above the background or average prey density delimited by a minimum threshold and an area of influence or attraction. It was assumed that if baleen whales search for the densest prey patches, the spatial overlap between blue whales and krill should be stronger with the densest portion of the patch and therefore should yield the greatest relative whale density.

We interpolated the density gradient of the acoustically-surveyed krill patches using ordinary kriging (ArcGIS®). From the raw acoustic data, it was clear that the krill patches generally followed isobaths, so anisotropy was applied to the kriging model in the alongshore direction to reflect this. The patch core was defined as the densest portion of the prey patch. Since the threshold for defining the 'densest portion' of a patch from a whale's perspective is somewhat arbitrary, several patch core densities were defined as the area of krill above a series of density thresholds. The density thresholds were defined between 4 to 128 $g \cdot m^{-2}$, doubling between levels.

To capture the attraction quality of a krill aggregation, we defined the area of influence of a krill patch as a series of spatial buffers around a patch core within which the density of whales was also estimated. Again, these buffers were determined somewhat arbitrarily as 3, 6 and 9 km surrounding a patch core, i.e. 0 km.

Based on previous findings about blue whale foraging behaviour in the SLE (Doniol-Valcroze et al. 2011, McQuinn et al. 2013b), we suspected that krill aggregation depth would be a significant factor in the choice of patches for foraging by blue whales. Therefore we conducted the same spatial analyses separately for the whole water column, i.e. to 220 m, and for the top 80 m.

In addition to the annual distribution maps, composite distributions of Arctic and northern krill aggregations were made from all 6 years of data. These composite mosaics were constructed by spatially merging the raster maps from each of the annual distributions while selecting the maximum value per pixel.

SPATIAL ASSOCIATION INDEX

To determine the extent of spatial association between blue whales and krill patches, we defined a spatial association index (*AI*), to measure the relative proportion of the total blue whale count associated with patches and to describe the pattern of association around a patch. The density of blue whales was determined from their intersection (count) within each kriged density surface. The index was estimated as the ratio of blue whale density within the patch core and each of its associated buffers relative to the density of a random distribution. Therefore, the density, $D_{SPi,j}$, of blue whales, S, in patch, $P_{i,j}$, defined by a given prey density threshold, j within the core and buffers, i was equal to:

$$D_{SPi,j} = N_{SPi,j} / A_{Pi,j}$$

where, $A_{Pi,j}$ = the surface area within the detection range of the observers of a prey patch and $N_{S,Pi,j}$ = the number of individual blue whales $S_{i,j}$ in prey patch, $P_{i,j}$. This patch-associated blue-

whale density was compared to the total density of blue whales within the observer detection range of the study area (random distribution):

$$D_{Sr} = N_s / A$$

where, A= surface area covered by the survey (MMOs) and N_S = total number of blue whales S in the survey. For this study, no correction was made for the decrease in detection rate with distance from the survey platform. We thus assumed that all whales within the estimated detection range of the observer were seen. The association index, AI_{SPi} for blue whales S and patch P with buffer i and catch core density j was estimated as:

$$AI_{SPi,j} = D_{SPi,j} / D_{Sr}$$

An $AI > 1$ reflects a concentrating effect, i.e. a density greater than random, $AI \approx 1$, indicates no difference from random and $AI < 1$ denotes an avoidance effect. Since a patch has an area of attraction greater than the area of the patch core itself, by estimating the AI for the buffers as well as the core, we obtained an appreciation of the concentrating effect produced by the patch.

RESULTS

KRILL AND BLUE WHALE DISTRIBUTION

Results from the six surveys permitted the construction of a cumulative mosaic of krill abundance for the survey area, for both Arctic (Fig 2a) and northern krill (Fig 2b), indicating the location of krill patches over the 6-yr period. Areas of increased krill density corresponded to the shelf and the slope area of the Laurentian Channel, which has been identified as the primary habitat for Arctic krill (McQuinn et al. 2015) in the GSL (Fig 2a). Northern krill was distributed from the slope into the channel basins further offshore (Fig 2b). Although northern krill can exhibit areal densities ($g \cdot m^{-2}$) equal to or higher than Arctic krill (McQuinn et al. 2015), they are distributed vertically over a greater depth range, producing lower volume densities ($g \cdot m^{-3}$), and thus are less concentrated for predators.

Likewise from the surveys, we found that the density of baleen whales was highest in the slope areas: the head of the Laurentian Channel (HLC), the Gaspé current (Matane, Cap Chat, Mont Louis, Petite Vallée and Rivière-au-Renard), east of Gaspé (ST8A), Banc Parent (ST10B) and Pentecote (Fig 1 and 2). Most of the blue whale sightings were outside the estuary and of those, the majority were along the Gaspé current (Fig 1 and 2; ST5-ST8A), with high occurrence also between Sept-Iles and Pointe-des-Monts at the north shore entrance to the estuary. In 2009 off Rivière-au-Renard in ST7 (Fig 1 and 3), there was a thin Arctic krill patch along the slope that attracted a variety of baleen whales, including the majority of the identified blue whales in that year.

SPECIES ASSOCIATION

Arctic krill:

Blue whale AI patterns varied among years. In 2009, blue whales showed a weak association (below random) with the densest patch density (128 $g \cdot m^{-2}$) of Arctic krill (Fig 5a) when considering the whole water column, i.e. 0-220 m. They showed a peak association (5-7 times random) with the 64 and 32 $g \cdot m^{-2}$ core densities as well as within the 3-km buffer of the 128 $g \cdot m^{-2}$ core density. The association dropped off close to or below random within 6-9 km from the core.

Blue whale *AI*s were below random for *T. raschii* at virtually all densities above 16 $g \cdot m^{-2}$ in both 2011 and 2012 (Fig 5b,c). Indeed in 2011, no sighted blue whale was associated with a krill patch, whether throughout the water column (Fig 3c &5b) or in the top 80 m (Fig 6b). However in 2011, abundances of *T. raschii* were at their lowest in terms of swarms, i.e. integrated surface area between 0-80 m (Fig 7a) as well as of overall annual biomass in the time series (Fig 8). As for 2012, only 6 blue whales were sighted, all at the mouth of the estuary on the north shore (Fig 9). Also, it is of note that during this survey, the visibility for the observers was particularly poor, i.e. reduced to nil along the entire south shore of the estuary along the Gaspé current to Gaspé (Fig 10c), significantly reducing the probability of sighting whales in this area. This was an area where several dense krill patches were measured acoustically (Fig 9) and where blue whales were sighted in all other years when observers were present. In 2013, the pattern of association was similar to 2009 (Fig 5d), when blue whales showed the highest *AI* (11 times random) with krill densities of 32 $g \cdot m^{-2}$ rather than in the highest core densities of 64 or 128 $g \cdot m^{-2}$.

Blue whale *AI*s for shallow patches (0-80 m) of Arctic krill were much higher relative to deep patches in 2009 and 2013 (e.g. more than 6 times higher in 2009), even though the maximum core densities were much lower, i.e. 32 $g \cdot m^{-2}$ vs 128 $g \cdot m^{-2}$ (Fig 5 & 6). In 2009, sighted blue whales associated with shallow patches or swarms resulted in a whale density 30 times random in the 3-km buffer of the 32 $g \cdot m^{-2}$ core density (Fig 6a) compared to 5-7 times random at a core density of 64 $g \cdot m^{-2}$ for the whole water column.

Finally, in 2013 the area occupied by shallow water swarms was as low as in 2011 (Fig 7a). However, blue whales were observed associated with these swarms, especially along the Gaspé Current (Fig 3e). This resulted in a high *AI* value whether with the whole water column (>11 times random at 32 $g \cdot m^{-2}$ core density; Fig 5d) or with the top 80 m (40 times random at 16 $g \cdot m^{-2}$; Fig 6d). Swarm densities greater 16 $g \cdot m^{-2}$ were not observed in this year.

Northern krill:

Compared to the association patterns seen with *T. raschii*, blue whale *AI*s were substantially lower with *M. norvegica*. Nowhere did the *AI* exceed 4 times random for a patch core ≥32 $g \cdot m^{-2}$ either for 0-220 m (Fig 11) or 0-80 m (Fig 12). The highest *AI* observed was in 2013 where it reached 8 times random in the 3-km buffer of the 128 $g \cdot m^{-2}$ core density for 0-220 m, similar to 2009 for *T. raschii*.

In 2009 there was an increased blue whale density estimate associated with the 9-km buffer at the 16 $g \cdot m^{-2}$ core density for 0-80 m (Fig 12a). Closer inspection showed that these were the same whales that were very highly associated with the 32 $g \cdot m^{-2}$ core density of *T. raschii* off Gaspé (Fig 3a and Fig 4a), implying that this was a spurious result. It is much more likely that the spatial correlation between Arctic and northern krill in this area was the source of this unexpectedly high *AI*, rather than an actual association between blue whales and this low core density of *M. norvegica*. In 2011 and 2012, there were very few surface swarms of northern krill (Fig 7b) and the *AI*s for blue whales were also very low, i.e. below random. In 2013, there were as many surface patches as in 2009 (Fig 7b), but again the *AI*s showed no association with blue whales (Fig 12d).

DISCUSSION

From this series of combined acoustic-MMO surveys, it is clear that blue whale habitat in the western GSL extends beyond the estuary and, in fact, is more prevalent throughout the northwestern GSL, at least during August. Our results showed that in general, blue whales in the northwestern GSL are more strongly associated with the density distribution of *T. raschii* than *M. norvegica*, despite the fact that *M. norvegica* is the larger of the two species. However,

this association was seen with densities below the highest core densities. In particular, we show that blue whales were specifically associated with shallow water Arctic krill swarms (0-80 m) more than all other krill configurations during daytime.

T. raschii formed higher patch densities, was distributed higher in the water column and, at least in 2009, comprised more biomass than *M. norvegica* (McQuinn et al. 2015), thus making more biomass available to air-breathing predators at a lesser energetic cost (Doniol-Valcroze et al. 2011). As such blue whales were found where Arctic krill were aggregated, i.e. in the shelf and slope areas of the Laurentian Channel (McQuinn et al. 2015).

However there were exceptions to this general pattern. In 2011, none of the 10 sighted blue whales was associated with krill patches, nor with surface swarms of either species. In that year, the overall biomass of *T. raschii* was at its lowest and, along with *M. norvegica,* the biomass within the upper 80 m was also the lowest in the time series, making krill swarms very rare and possibly difficult for predators to locate. Notwithstanding, in 2013 Arctic krill abundance within the upper 80 m was as low as in 2011 (Fig 7a) and the *AI* for these patches was quite high, suggesting that blue whales were able to locate them in this year. Also in 2013, the *AI* was relatively high for *M. norvegica* for the whole water column (Fig 11d), although not for surface swarms (Fig 12d). Again, surface swarms of *T. raschii* were rare in this year and its total biomass was lower than northern krill (Fig 8).

In 2012, only 6 blue whales were sighted, again none of which were associated with krill patches despite a relative abundance of shallow Arctic krill swarms (0-80m) similar to 2009. However, due to the particularly poor observer visibility that year when surveying the krill patches along the south shore of the estuary, any blue whales exploiting these patches would have been missed by the observers. Limited vessel time means that we could not choose only favourable conditions when surveying.

In conclusion, blue whales were attracted to areas of high density patches especially of Arctic krill, but foraged in the area of lower density surrounding the core. This suggests that blue whales do not necessarily exploit areas of highest biomass or the highest areal density of krill aggregations, but rather areas of highly accessible krill biomass of which shallow-water, daytime swarms are disproportionately selected.

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FIGURES

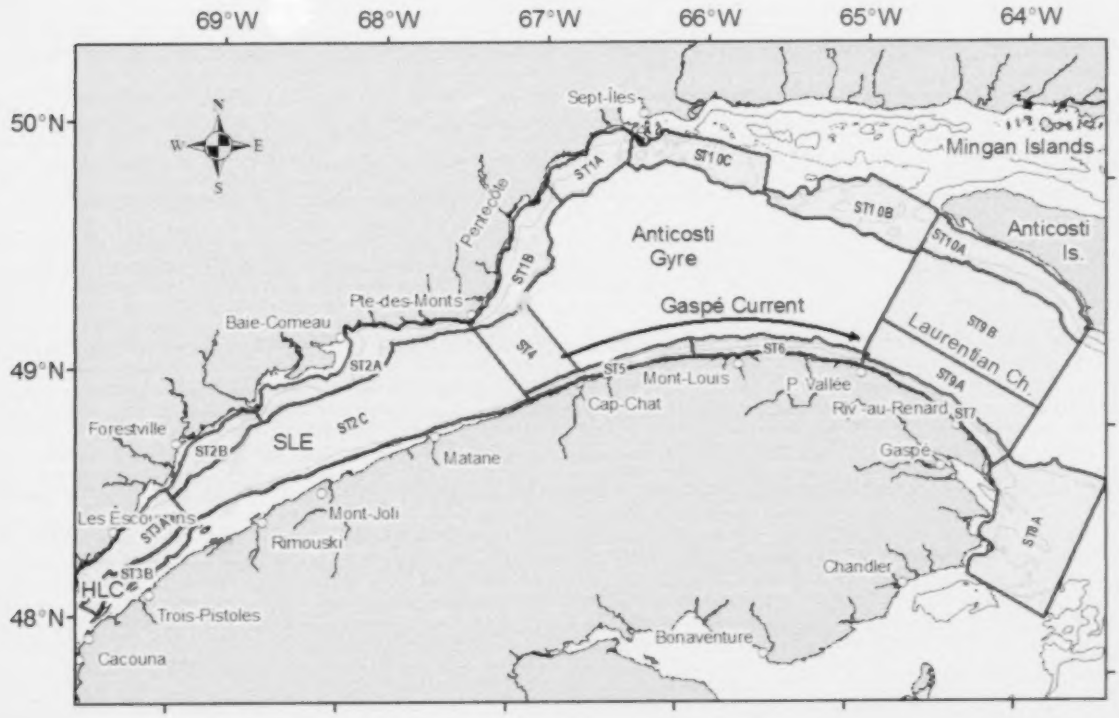

Figure 1. Study area showing the survey design in 2009. Statistical strata are shown in light grey. From 2010, the strata were expanded to cover from the Mingan Archipelago (north of Anticosti Island) to Sept-Îles.

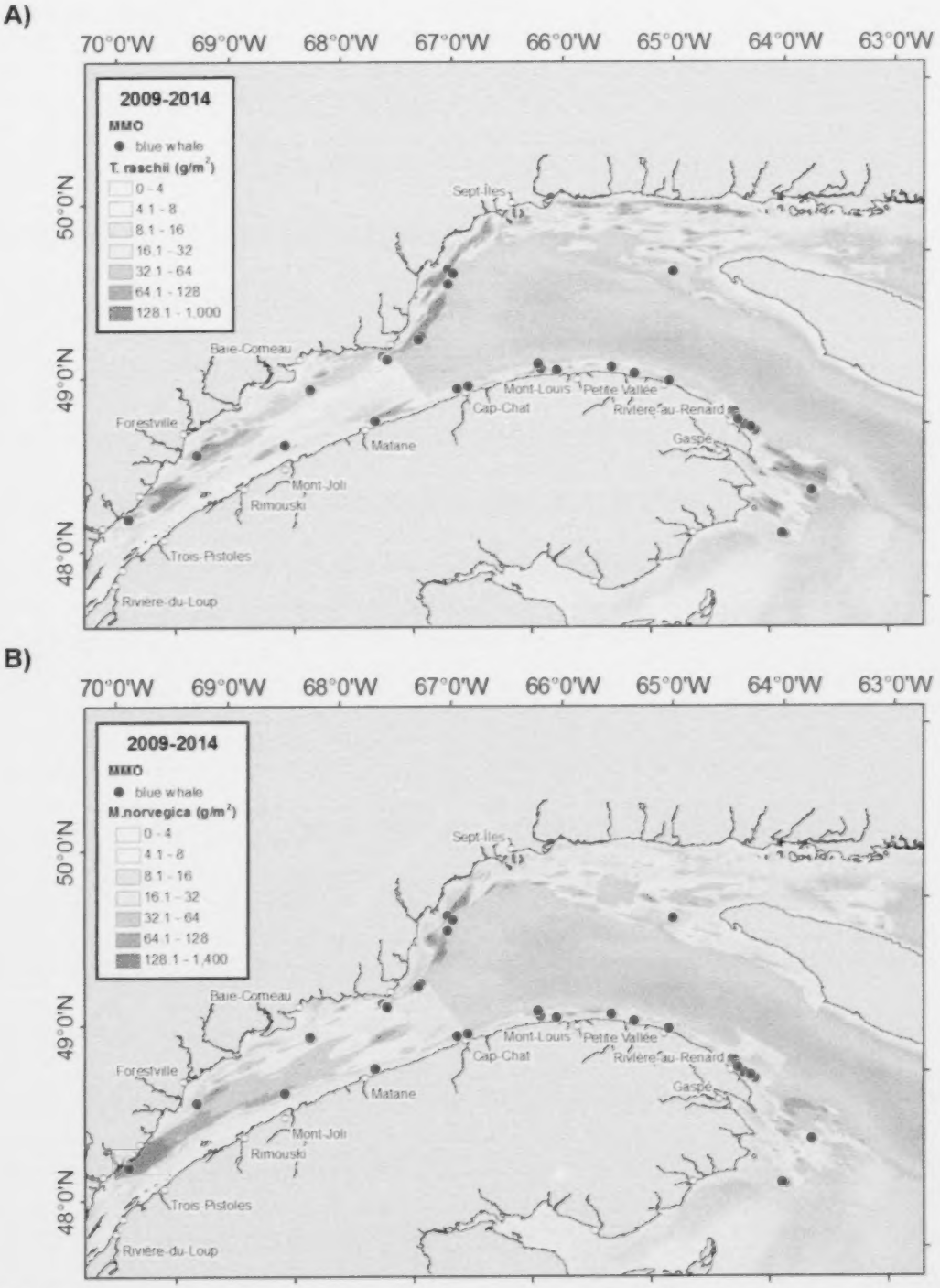

Figure 2. Mosaic of (a) Arctic krill (T. raschii) and (b) northern krill (M. norvegica) maximum annual density and blue whale sightings (blue dots) from combined MMO-acoustic surveys conducted between 2009 and 2014.

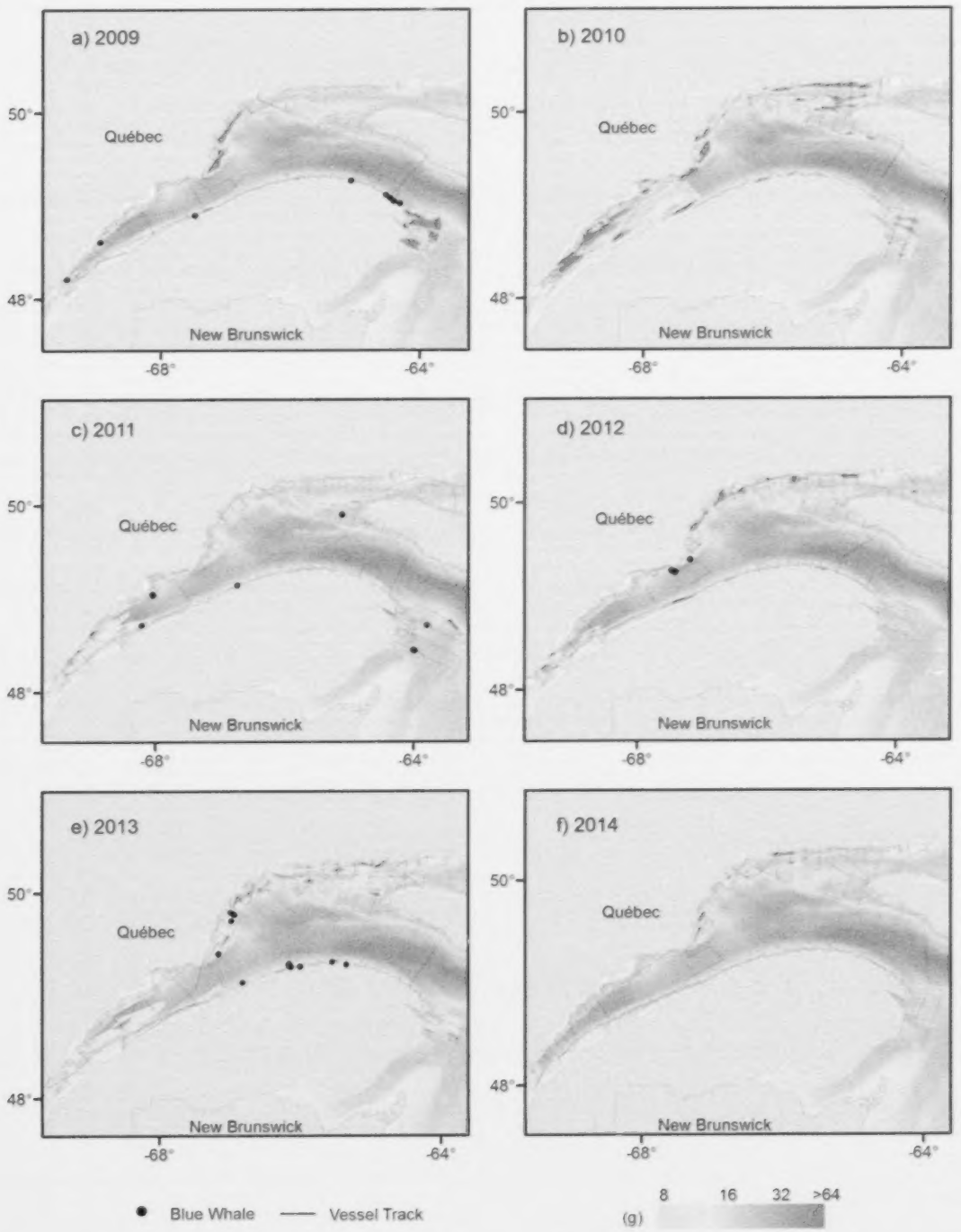

Figure 3. T. raschii. Annual krill density (g·m^{-2} between 0-220 m) and blue whale sightings (black dots) from combined MMO-acoustic surveys conducted between 2009 and 2014 (a-f).

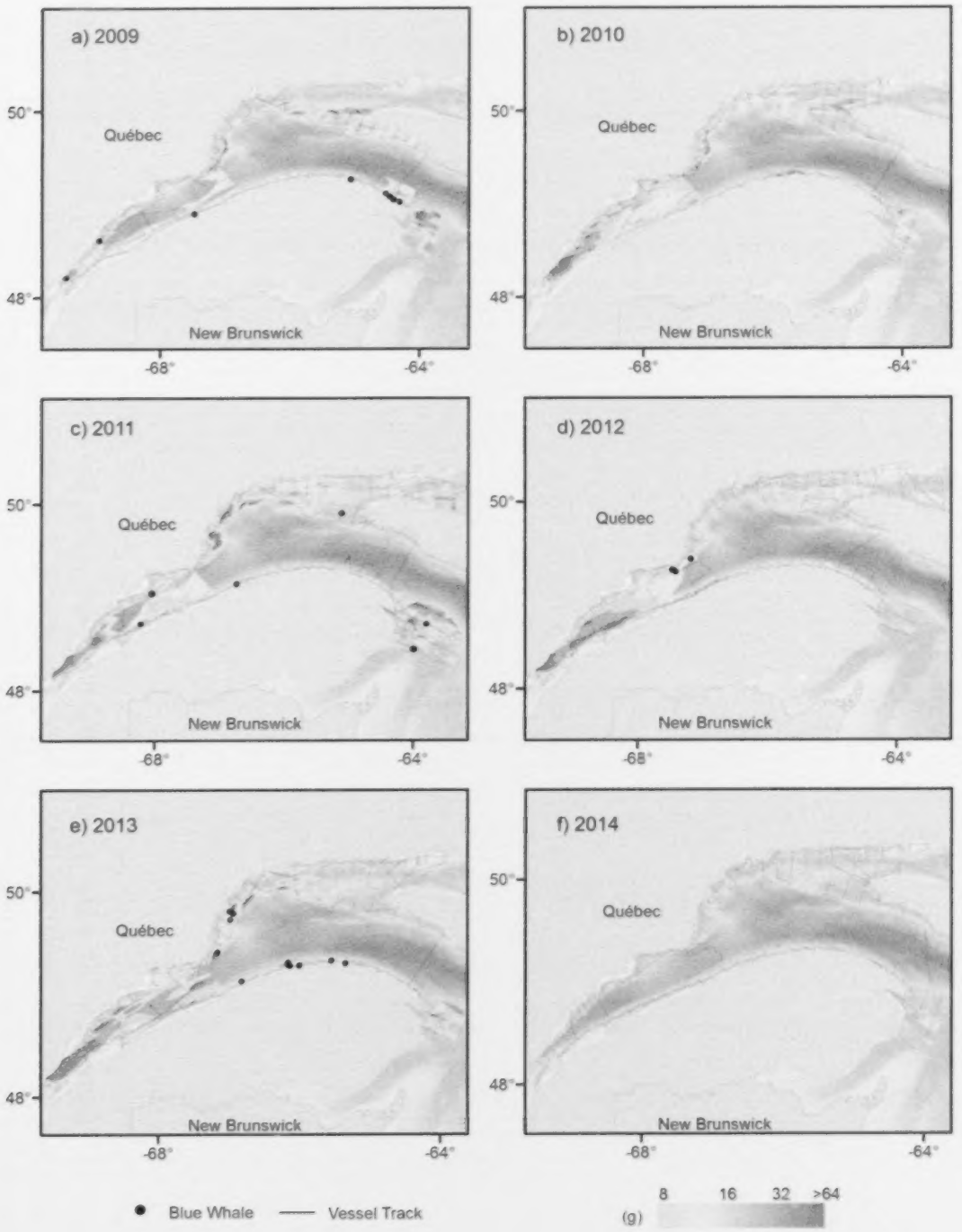

Figure 4. M. norvegica. Annual krill density (g·m^{-2} between 0-220 m) and blue whale sightings (black dots) from combined MMO-acoustic surveys conducted between 2009 and 2014 (a-f).

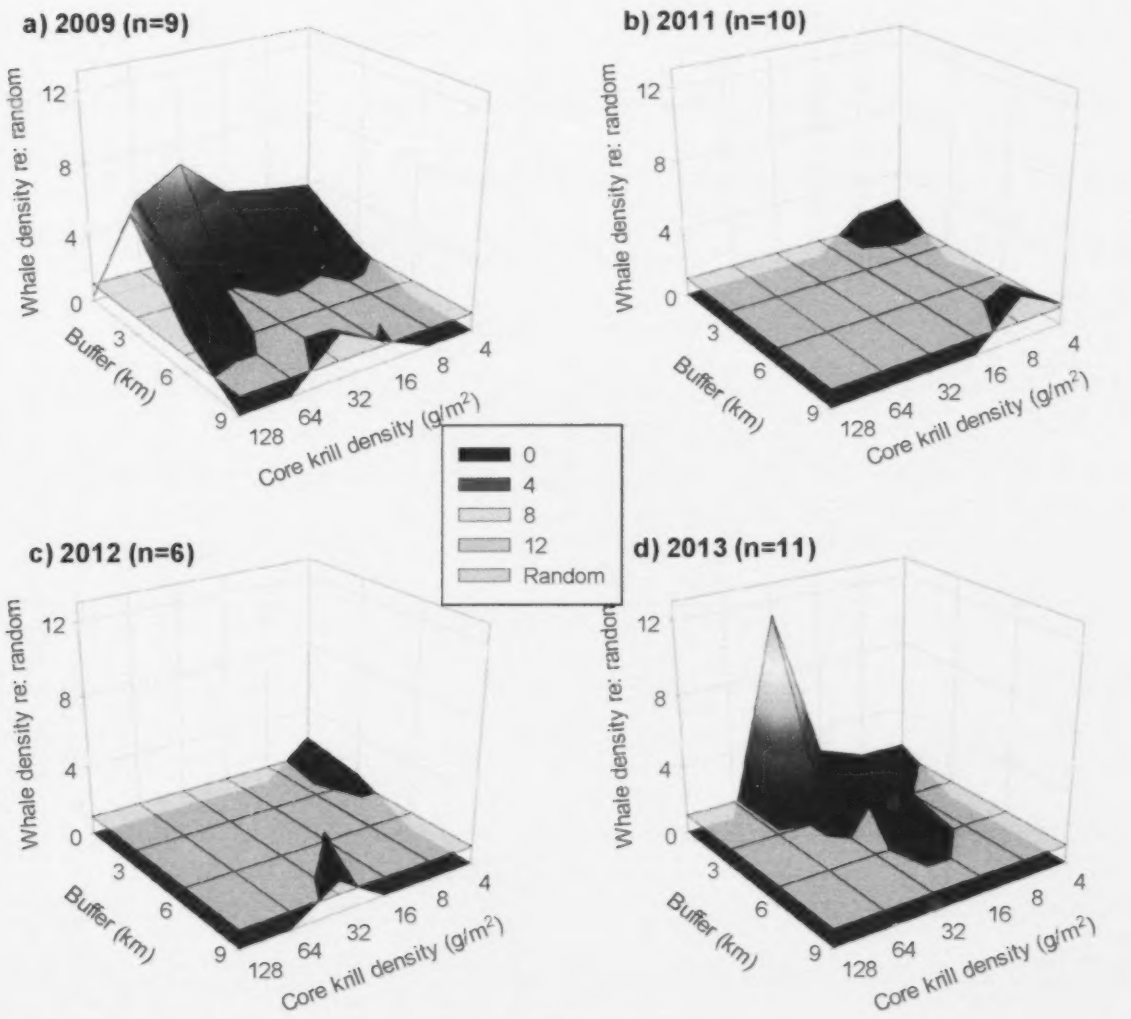

Figure 5. T. raschii between 0-220m. Association index estimated as the ratio of blue whale density within a prey patch core and each of its associated spatial buffers relative to a random density distribution for (a) 2009 (b) 2011 (c) 2012 and (d) 2013.

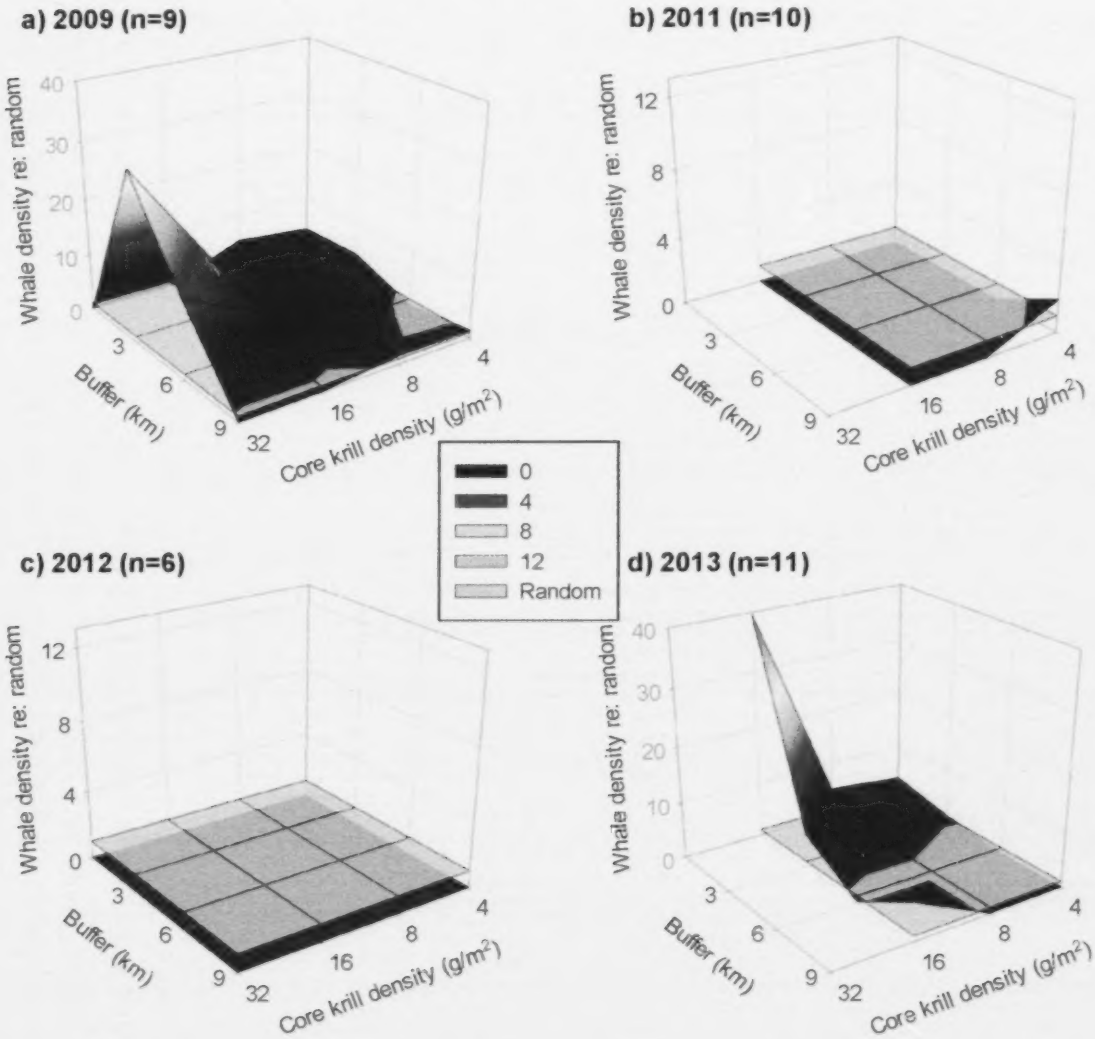

Figure 6. T. raschii between 0-80m. Association index estimated as the ratio of blue whale density within a prey patch core and each of its associated spatial buffers relative to a random density distribution for (a) 2009 (b) 2011 (c) 2012 and (d) 2013. Colour scale applied to 2011 and 2012.

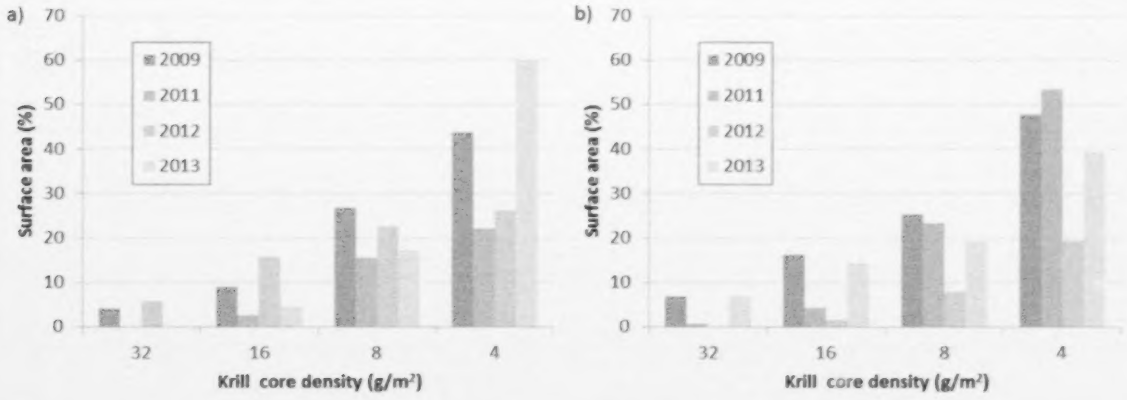

Figure 7. Surface swarms 0-80 m. Percentage of the total surface area surveyed that was occupied by (a) Arctic krill and (b) northern krill shallow-water swarms with core densities ranging between 32 and 4 g·m^{-2} between 2009 and 2013.

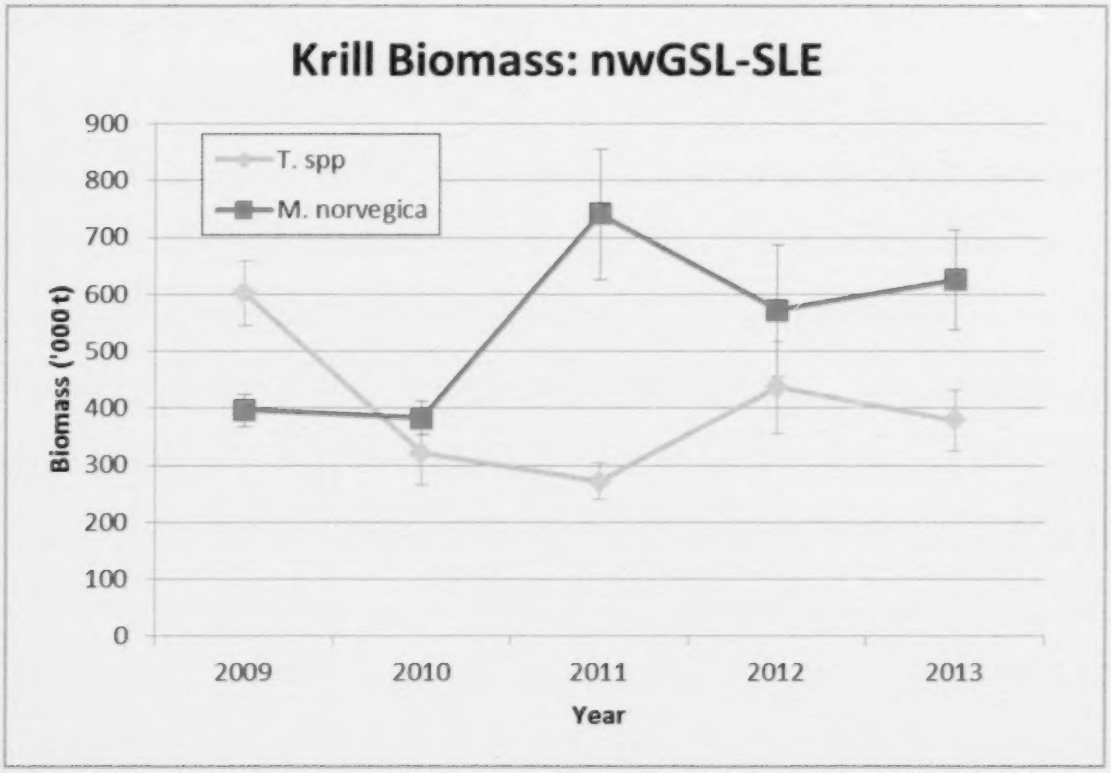

Figure 8. Thysanoessa spp. and M.norvegica. Total biomass estimated for northern and Arctic krill (T. raschii and T. inermis combined) from annual August acoustic surveys in the nwGSL-SLE.

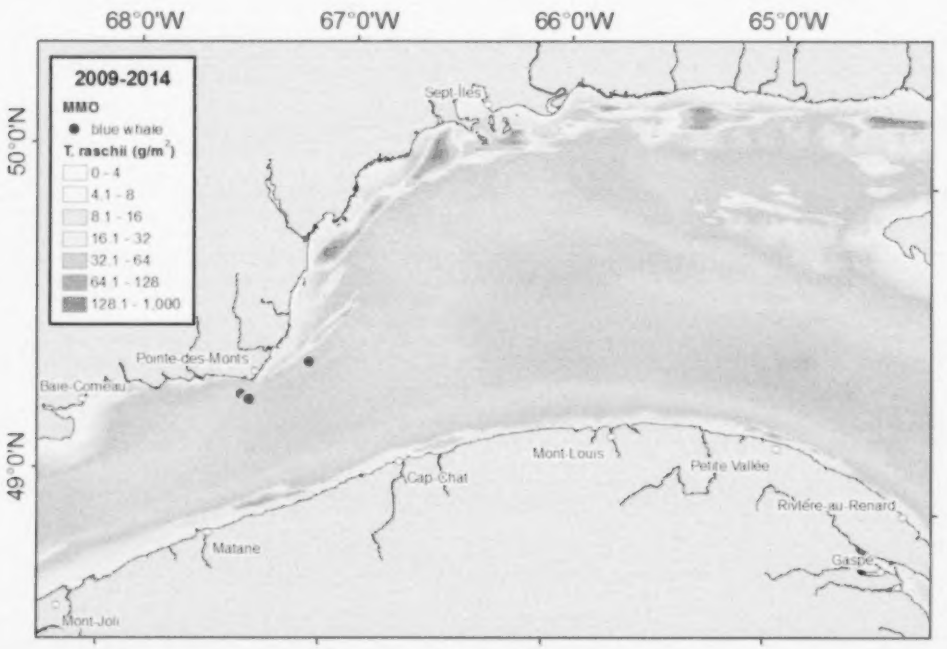

Figure 9. T. raschii. Close-up of annual krill density (g·m^{-2} between 0-220 m) and blue whale sightings (blue dots) from combined MMO-acoustic surveys conducted in 2012.

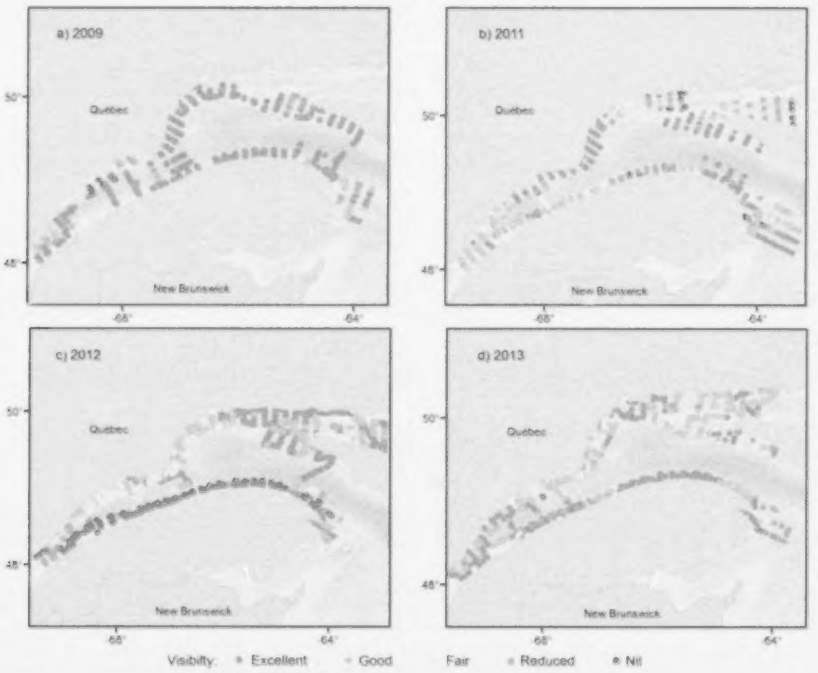

Figure 10. Observer visibility. Coded visibility index from excellent (green) to nil (red) for each annual MMO-acoustic survey from (a) 2009 (b) 2011 (c) 2012 and (d) 2013.

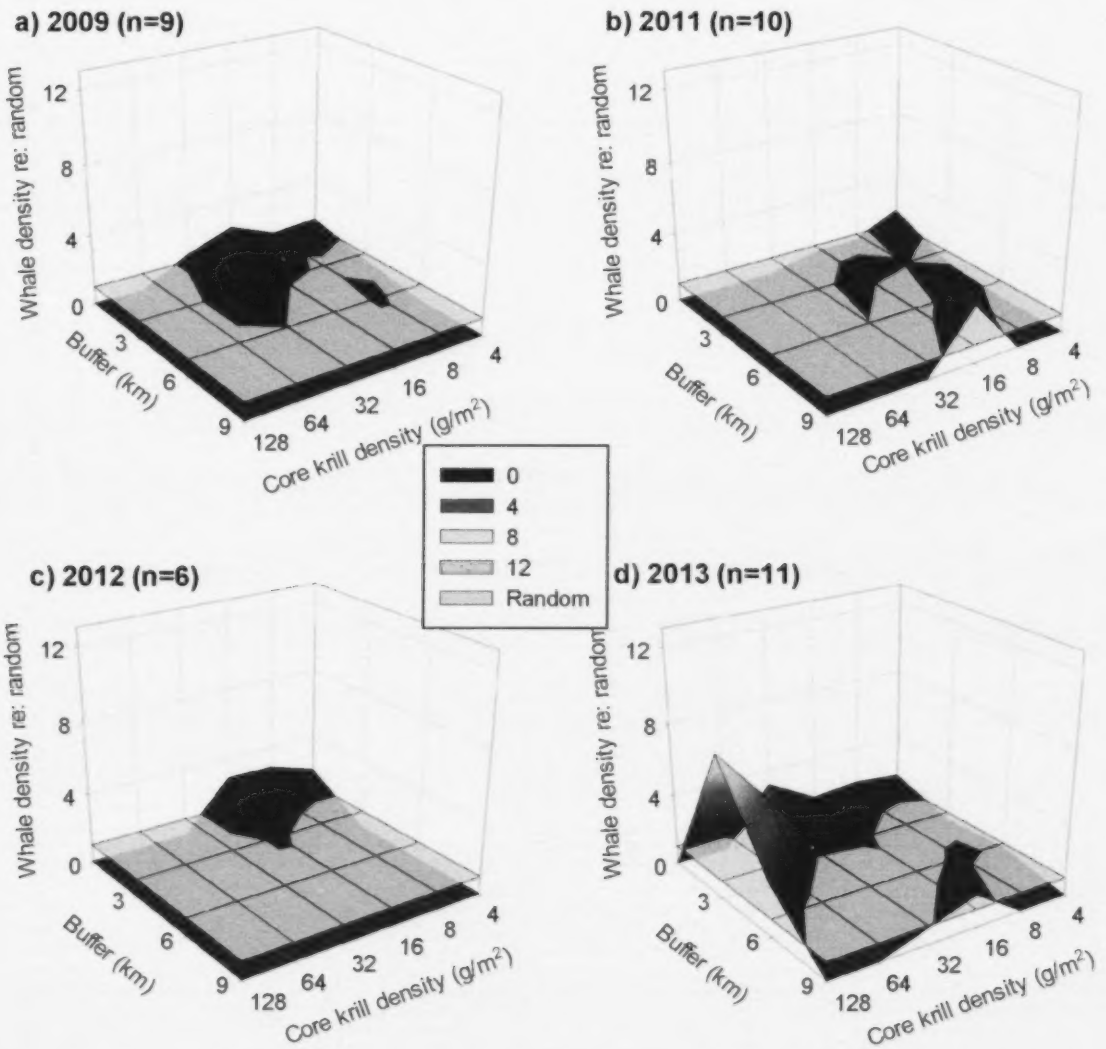

Figure 11. M. norvegica between 0-220 m. Association index estimated as the ratio of a given whale species density within a prey patch core and each of its associated spatial buffers relative to a random density distribution.

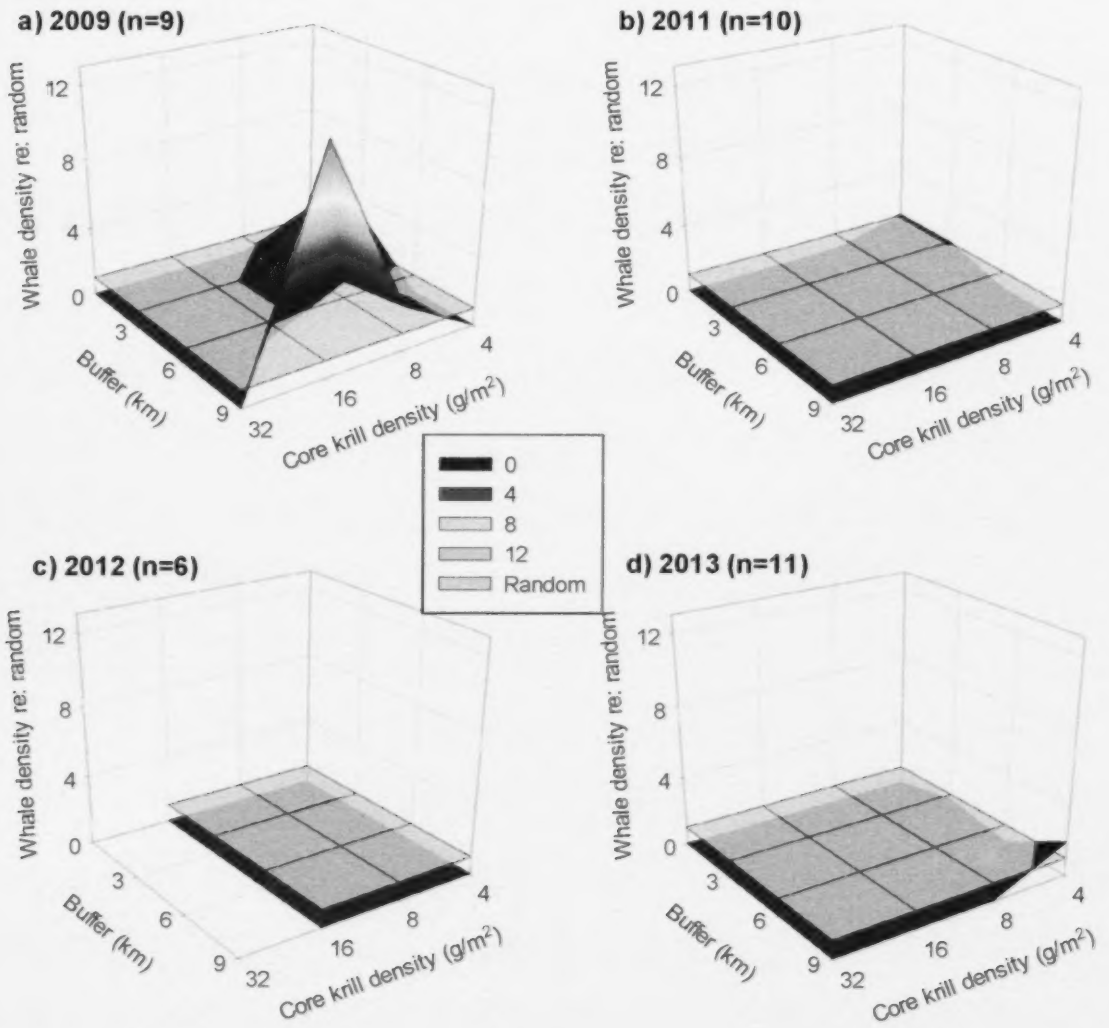

Figure 12. M. norvegica between 0-80 m. Association index estimated as the ratio of a given whale species density within a prey patch core and each of its associated spatial buffers relative to a random density distribution.